SEASONAL AND ANNUAL VARIATIONS IN THE ATTACHMENT AND SURVIVAL OF BARNACLE CYPRIDS [1]

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Two factors governing the development of a barnacle population have been investigated: namely, the number of barnacle cyprids attaching daily and the relationship of the daily cyprid accumulation to the number of adult barnacles attaching per month in Biscayne Bay, Miami Beach, Florida. On surfaces exposed for one month at this location, adult barnacles were invariably the dominant organism. No competition by other forms developed in this time interval to limit significantly the attachment of barnacles or their growth. This study was therefore concerned with numbers of cyprids settling daily, survival of cyprids, seasonal growth rates and space limitations, as factors affecting the size of the month-old barnacle population.

The survival of barnacles following attachment has been studied principally by Moore (1934), Hatton (1938) and Moore and Kitching (1939) with respect to the attachment of *Balanus balanoides* and *Chthamalus stellatus* to cleaned rock surfaces in the intertidal zone. These investigations were interested mainly in the effect of tidal level, exposure to surf and to sun, and interspecific competition on the growth and mortality of intertidal barnacles. Their findings are not directly applicable to barnacles attached to continuously submerged surfaces since they emphasize the effect of tidal exposure. The investigations of van Breemen (1933) on the survival of barnacles attached to continuously immersed surfaces considered the ultimate age of specific species.

METHODS

To ascertain the numbers of barnacle cyprids attaching daily, a collecting surface of smooth, black glass was hung in the waters of Biscayne Bay at the Beach Boat Slips, Miami Beach, Florida, just below the low-tide mark. The cyprids which attached to one side of the glass (500 sq. cm.) during each 24-hour period were counted daily between 8:00 A.M. and 8:15 A.M. The surface was wiped clean after each counting. Temperature and density of the surface water were also determined at the same time. From these data salinity was calculated. The investigation was carried out over a period of 38 months, except for short interruptions in the summers of 1943, 1944 and 1945.

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During the same period, monthly fouling attachments in Biscayne Bay were also reported. These fouling collections were made on clear glass panels, backed with a dark red paint, of the same area as the cyprid collecting surface. The dark red backing provided a substratum color which was comparable to the black glass (Visscher and Luce, 1928). A total of 74 monthly collections were made, panels being immersed every 15 days for 30 days of exposure. From the monthly attachment of assorted fouling forms the barnacle count was extracted for comparison with the sum of the daily cyprid attachment for the same month. *Balanus improvisus* was the dominant adult barnacle on the monthly collectors and presumably was responsible for most of the cyprids (Weiss, 1948).

Results

The daily records of cyprid attachment, water temperature and salinity are presented in Figures 1, 2 and 3, respectively. Three-day moving averages were employed in plotting these data, for the purpose of minimizing random fluctua-

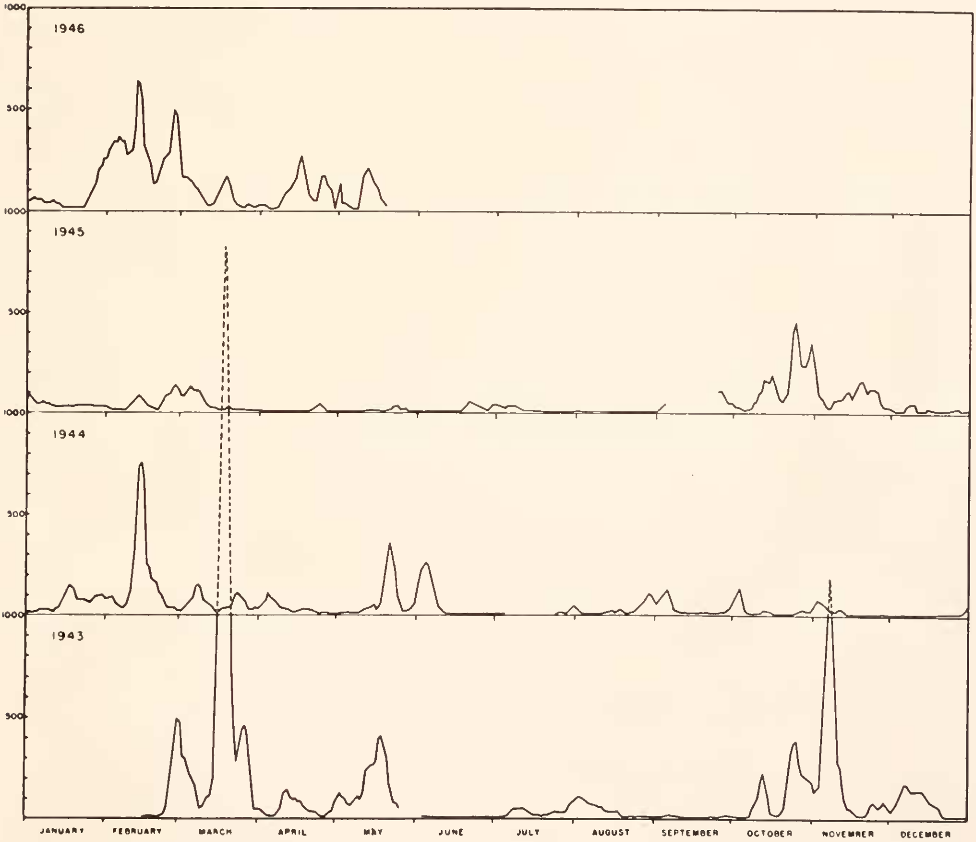

FIGURE 1. The daily accumulation of barnacle cyprids on black glass (500 sq. cm.) at the Beach Boat Slips, Miami Beach, Florida, February 1943–May 1946, plotted as a three-day moving average.

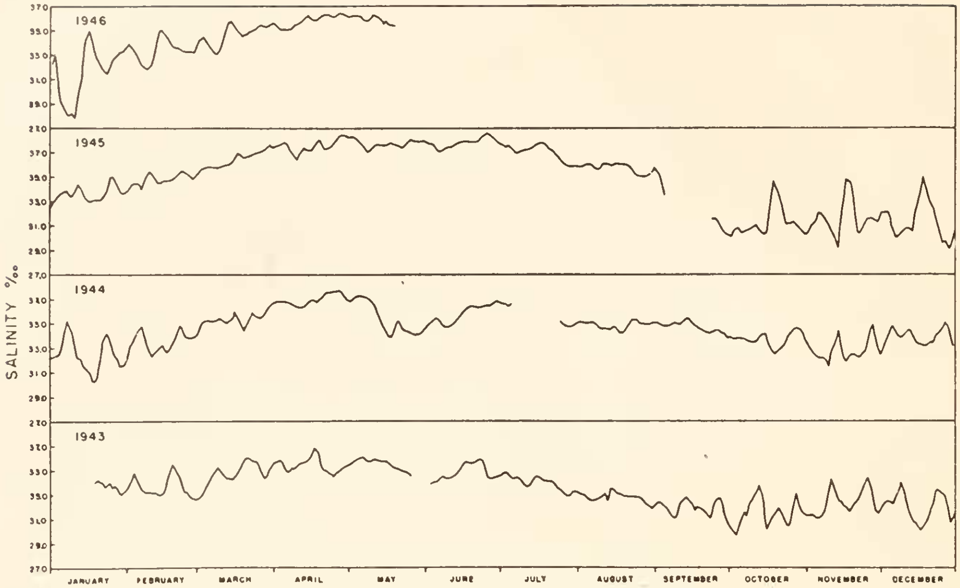

FIGURE 2. The daily salinity record of Biscayne Bay made at the Beach Boat Slips, Miami Beach, Florida, plotted as a three-day moving average.

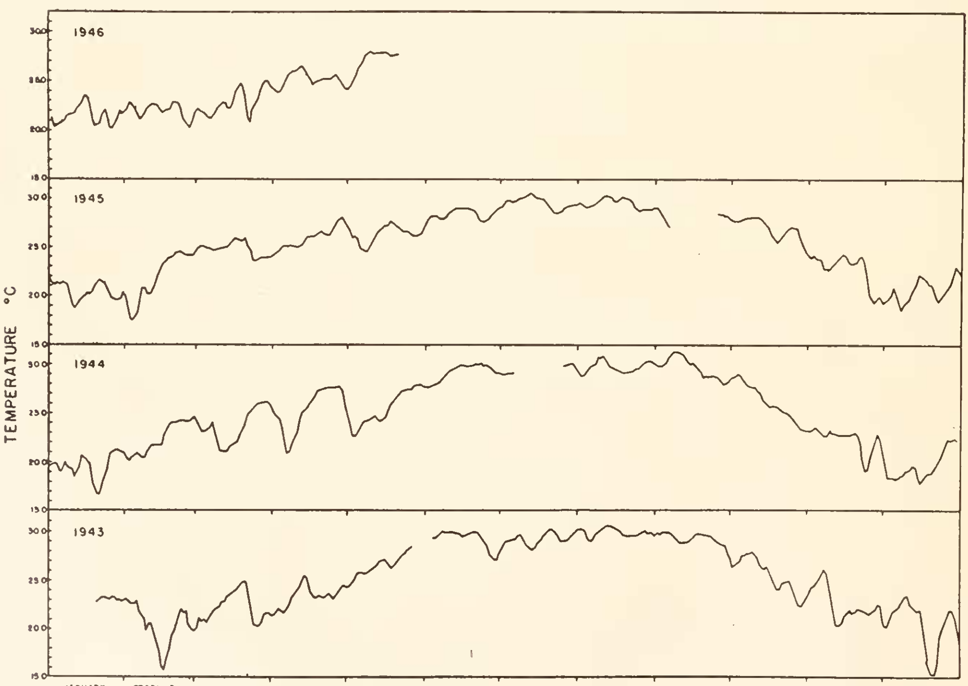

FIGURE 3. The daily temperature record of Biscayne Bay made at the Beach Boat Slips, Miami Beach, Florida, plotted as a three-day moving average.

tions. Both the temperature and salinity of Biscayne Bay showed seasonal variation. The temperature fluctuated each year between approximately 16° C. and 30° C. The salinity showed an annual range from approximately 28.00 ‰ to 37.00 ‰, the peak coinciding with the end of the dry season. This period occurred each year between April and June. With the onset of the summer rains, the bay salinity declined, reaching its minimum in the period from October to January. During this period, and to a lesser degree in the month preceding and following, the salinities showed marked short-period fluctuations, which were indicative of the stage of tide at which the water sample was taken. A sample taken at high tide was always more saline than one sampled at low tide. This fluctuation of salinity was most pronounced during the rainy season, when the surrounding land areas were well soaked and the fresh water run-off from the land diluted the bay water. Slight tidal variations in salinity were evident even in the period of maximum salinity, but the range was not as great. Temperature fluctuations paralleling the tidal cycle were also evident due to the more rapid warming and cooling of the comparatively isolated bay water.

Barnacle cyprids settled on every day but three during the 38 months of observation. The numbers attaching daily varied from as low as 1 or 2 to a maximum of over 2800 per 500 sq. cm. In general, the settling of cyprids was characterized by peaks in attachment at relatively frequent intervals. Nevertheless, there was no apparent relationship between the sizes of successive peaks and the interval between the peaks, which ranged in most cases from 7 days to a month.

Several peaks of cyprid attachment occurred in the early spring and late fall of each year, but these peaks showed considerable variation from year to year in both magnitude and exact time of occurrence. The period from June to September was characterized by low daily cyprid attachments and a few small peaks, if any. However, in 1945 this period of reduced daily attachment extended from the middle of March to September. The spring peaks of attachment were generally greater than those of the fall; but in 1945 this pattern was reversed, the fall peaks being greater. The spring peaks in 1946, although large, were not as great as in 1943 and tended to extend over a longer period.

For the purpose of ascertaining the mechanism controlling the periodic rises in cyprid attachment, these fluctuations were analyzed with respect to changes in the temperature and salinity of the bay water. Since the barnacle cyprid follows after a series of six nauplii stages, fluctuations of its attachment were also examined with respect to changes in the marine environment taking place at the time of release of the nauplii into the plankton. A search of the literature failed to reveal the duration of the free-swimming period for *Balanus improvisus*. However, of the species that were studied (Table I), the free-swimming periods ranged from 7 days to 3½ weeks.[3]

Assuming intervals of one, two or three weeks between spawning and settling, no satisfactory correlations were found between changes in temperature and salinity and the periodic peaks in cyprid settling. The only relationship evident was between the seasonal increases in numbers settling and the temperature. The rises

[3] The period of time that the cyprid spends in the plankton prior to settling was noted quantitatively by Willemoes-Suhm (1876), who studied the development of *Lepas fascicularis*. In addition to observing six nauplii stages, he noted that the "cyprid evidently attaches itself on the very first occasion."

TABLE I

Time for development through nauplii stages to cyprid

Barnacle species	Number of nauplii stages	Time for development to cyprid
Balanus crenatus Bruguiere [1]	6	7–10 days
Balanus crenatus Bruguiere [2]	8	13–14 days
Balanus eburneus [3]	6	7–10 days
Balanus perforatus Bruguiere [4]	6	21 days
Chthamalus stellatus [5]	6	18–20 days
Verruca stroemia [5]	6	23–27 days
Balanus balanoides [5]	6	3–3½ weeks

[1] Bohart (1929).
[2] Herz (1933).
[3] Grave (1933).
[4] Lochhead (1936).
[5] Bassindale (1936).

in cyprid numbers in the spring and autumn occurred between the periods of minimum and maximum temperatures. This relationship suggested that *Balanus improvisus* breeds in a temperature range of approximately 18° C. to 27° C. The temperature above which breeding diminished greatly or ceased was more clearly defined than the minimum temperature limit. The waters of Biscayne Bay exceeded the upper temperature breeding limit for several months each year, but rarely and only for short periods did the temperature drop below the lower breeding limit.

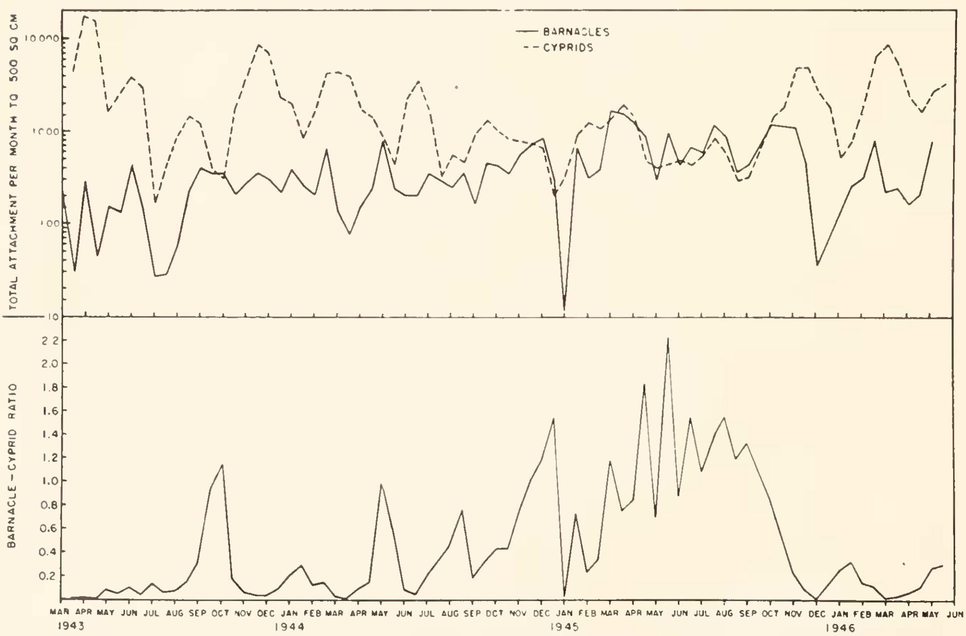

FIGURE 4. The monthly totals of daily cyprid settling and the monthly barnacle attachments on glass surfaces (500 sq. cm.), upper half. The ratio of barnacles to cyprids attached in each monthly period, lower half.

The numbers of barnacles found on the monthly collectors showed considerable variation, as indicated in Figure 4. For the entire period of observation the monthly barnacle collections dropped below 100 only eight times and went above 1000 only six times. The extreme numbers of barnacles collected in one month were 10 in December 1944 and 1615 in February 1945. However, extreme fluctuations in numbers of barnacles did not usually occur in two successive collections but followed a period in which a trend of rising or falling numbers was evident. Although not as marked, a rising trend in the monthly collections of barnacles during the period of 1943–1945 was observed, reaching a peak simultaneously with the low point of the monthly totals of cyprids.

Of the varying numbers of cyprids attaching daily it was assumed that all or some portion metamorphosed and grew to adult size. For comparison with the monthly barnacle collections the daily cyprid attachments were totaled every 15 days for the preceding 30-day period. The monthly cyprid totals, in general, showed a greater fluctuation than the monthly barnacle collections, as indicated in Figure 4. During the 38 months of observation, the numbers of cyprids attaching in a month decreased to a minimum in 1945 and then rose once more. This fluctuation is more clearly indicated in Table II, in which the number of monthly

TABLE II

Number of monthly cyprid totals greater and less than 1000 in six-month periods

Period	>1000	<1000
March 15, 1943–September 1, 1943	9	3
September 15, 1943–March 1, 1944	9	3
March 15, 1944–September 1, 1944	6	6
September 15, 1944–March 1, 1945	4	8
March 15, 1945–September 1, 1945	2	10
September 15, 1945–March 1, 1946	9	3

cyprid totals greater than 1000 are compared with the number of monthly totals less than 1000 for six-month periods. The number of monthly cyprid totals of less than 1000 reached a maximum in the period from March 15, 1945 to September 1, 1945. The concurrence of a high proportion of monthly cyprid totals less than 1000 with a period of maximum barnacle collections suggests that conditions for survival and maturity of the cyprid were optimum when the daily rate of attachment totaled 400 to 1000 per month (Fig. 4, upper half).

However, there were five occasions when the monthly cyprid totals in this range were not paralleled by monthly barnacle collections indicative of good survival. Since three of these collections were in the summer and two in the winter, it was not possible to identify these anomalies with a particular temperature condition or any other specific phenomenon. Cyprid totals of 2000 or more, which were found in 25 out of 74 monthly summations, invariably resulted in high mortality and poor survival. These data have been graphically presented by Deevey (1947) in a recent review of natural populations of animals. The phenomenon of attachment of enormous numbers of cyprids and high mortality was attributed by Moore (1935) to depletion of the stock of food in the water by the extra-large population. It should be pointed out that there were several occasions, particularly in 1945, when monthly cyprid totals slightly greater than 1000 were paralleled by large barnacle collections.

The ratio of the monthly totals of barnacles to cyprids is presented in the lower half of Figure 4. As shown, a ratio of 1 indicates survival of all attaching cyprids, and values less than 1 indicate the degree of survival (and mortality) of the cyprid population. In addition, there is the anomalous condition of ratios greater than 1, which indicates more adult barnacles at the end of a month than the total of settling cyprids in the same period.

The survival ratio was greater than 1 in October 1943, May and December 1944, and on nine of the monthly collections in 1945. A satisfactory explanation of this unusual condition may be found in the thesis of Phelps (1942) and of Scheer (1945) that the bacterial slime film, which forms on surfaces submerged in the sea, provides an environmental condition more suitable for attachment and growth than a clear bare surface. The daily collector, wiped clean every morning, may not have been as attractive a surface for attachment as the collector continuously immersed, which permitted a slime film to form within a few days after immersion.

During the period of observation, a distinct tendency toward greater survival of the cyprids was observed, reaching a peak in 1945 and then decreasing sharply. Although occasional rises of the barnacle-cyprid ratio were indicative of good survival in 1943 and 1944, the year 1945 was by far the best survival year.

Another factor limiting the survival of barnacles was the area available for growth on the collecting surface. The maximum adult population, one month old, was obtained during February 1945 when 1615 barnacles filled the collector. On many other occasions, particularly during the summer months when the growth rate was highest (Weiss, 1948), considerably fewer barnacles, for example 525 in June 1945, filled the same collecting area. Thus the area available for barnacle attachment was limited by the rate of growth of the barnacles initially attached.

Summary

1. The daily barnacle cyprid attachment in Biscayne Bay, Florida, and concomitant water temperature and salinity measurements were recorded continuously during a period of 38 months.

2. No relationship between the frequent peaks in cyprid settling and changes in temperature and salinity was established.

3. Seasonal periods of heavy cyprid attachment were observed to occur within a temperature range from 18° C. to 27° C.

4. The survival of cyprids increased gradually from 1943 to 1945 and then decreased sharply, as shown by a comparison of monthly barnacle collections with monthly totals of daily cyprid attachments.

5. Seasonal variation in growth rates was observed to be an important factor in limiting the numbers of barnacles attached per unit area.

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